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Pan-Arctic diel vertical migration during the polar night

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ABSTRACT: Diel vertical migration (DVM) has generally been assumed to cease during the polar night in the high Arctic, although recent studies have shown the occurrence of lunar vertical migrations (LVMs) and shallow DVMs. Here, we quantified when and where full-depth (>20 m), solar-mediated DVM exists on a pan-Arctic scale. We observed the scattering population, most likely to be comprised of zooplankton, using 300 kHz acoustic Doppler current profilers (ADCPs). We quantified the presence/absence of DVM, and found that DVM continues throughout the year to at least 20 m at all locations south of 74° N. North of 77° N, DVM ceases for a period of time during the polar night. The dates of this cessation accurately align with the date of the winter solstice (±2 d). Between 74 and 77° N, DVM presence/absence is variable. Acoustic data sampled at 89° N, however, showed no evidence of DVM at any time during the year — a new observation. Using indicators of presence/absence of sea ice from ADCPs and satellite-derived sea ice concentration data, we revealed that local variations in sea ice cover directly determine the continuation or cessation of DVM during the polar night. Earlier-forming and higher-concentration sea ice causes a cessation in DVM, whereas low-concentration or late-forming sea ice results in continuous DVM when comparing migrations at similar latitudes.

KEY WORDS: Arctic · Diel vertical migration · Polar night

INTRODUCTION

Diel vertical migration (DVM) is an adaptive behaviour regulated by light, and has previously been thought to exist worldwide (Hays 2003). For zooplankton that feed in the surface layers, such as those feeding on phytoplankton, there will always be a trade-off between predation risk and the necessity to feed. Importantly, as long as there is a diel cycle in solar illumination, this trade-off will shift between day and night, with an increased risk of predation during daytime. Consequently, with varying solar illumination, there is typically an optimal time to feed at the surface (night) and an optimal time to migrate down to depth to hide from visually feeding predators (day); see Hays (2003) and Ringelberg (2010) for extensive reviews. It is generally accepted that the overall risk of visual predation is the predominant adaptive reason for DVM (Ringelberg 1999, Ringelberg & van Gool 2003), with light initiating and mediating the behaviour, and the durations of migrations linked to the duration of the daily photoperiod (day length). Additionally, the depth extent of DVM linearly correlates with the Secchi disk depth and therefore the vertical extent of surface illumination (Dodson

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1990), whilst the time spent at the surface feeding is correlated with the length of the night (Hays 1995). DVM behaviour can vary according to changes in predator composition, abundance, and distribution (Bollens & Frost 1991, Dale & Kaartvedt 2000, Berge et al. 2014). DVM has further implications by structuring ecosystems through predator–prey interactions and by increasing the flux of carbon to depth via the biological pump (Steinberg et al. 2000, Ducklow et al. 2001, Darnis et al. 2017).

At high latitudes, the extreme seasonal variation in solar altitude results in the polar night — a time during which the sun remains at or below the horizon throughout the entire 24 h diel cycle. However, the polar night in the Arctic is not homogenous in its intensity (Berge et al. 2015), and becomes longer and darker with increasing latitude. The most extreme diel cycle is found at the geographic North Pole (90° N) where there is just one sunrise and one sunset each year. The latitudinal increase in the extent of darkness is the result of the latitudinal variation in amplitude of the daily solar altitude cycle, which decreases linearly from 60° at 60° N, to 0° at 90° N (but remains constant at any given latitude throughout the year). Additionally, sea ice and snow cover modify the light environment, particularly through shading, which alters zooplankton vertical distribution and behaviours (Wallace et al. 2010). Although sea ice thickness and duration of presence generally increases at higher latitudes, local oceanic and meteorological conditions result in considerable spatial variation in the timing and thickness of sea ice cover even within the same latitudinal range, with large variation at small spatial and temporal scales. Solar irradiance and sea ice variation therefore contribute to a highly variable underwater light environment in the Arctic, which is anticipated to affect migration behaviours.

Our understanding of DVM is challenged in high latitude environments experiencing the polar night, as DVM is a light-driven behaviour. Indeed, it was previously assumed that DVM would cease entirely at high latitudes (Berge et al. 2009). Berge et al. (2009) found the first evidence of synchronised vertical migrations persisting throughout the polar night in Kongsfjorden, Svalbard (79° N), and this has since been confirmed on a pan-Arctic scale (Last et al. 2016). However, most of these migratory behaviours occur only for relatively short periods of time (order of several days), such as lunar vertical migrations (LVMs) during the full moon (Last et al. 2016), or are migrations with limited vertical amplitude that occur in the shallowest depth layers (<20 m) (Ludvigsen et al. 2018). These behaviours therefore have reduced consequences for wider ecosystem interactions or transport of carbon to depth. Much of the ecological polar night research has focused on migrators' responses to light cues other than the sun, including bioluminescence (Berge et al. 2012, Cronin et al. 2016) and the moon (Berge et al. 2009, Webster et al. 2015, Last et al. 2016).

Detection of DVM is commonly undertaken using bioacoustical methods (Brierley 2014). However, acoustic data sampled using acoustic Doppler current profilers (ADCPs) can only be used to detect migrations at a population level, when synchronised movements are recorded as migrating sound-scattering layer(s). During the period of midnight sun, when the sun remains above the horizon for periods longer than 24 h, unsynchronised migrations occur where zooplankton migrate on an individual basis rather than being controlled by a uniform underlying cue (Cottier et al. 2006, Wallace et al. 2010). Whilst unsynchronised behaviours might occur during the polar night, this study focused on the synchronised DVM behaviour that occurs at a population level ('classic DVM' as defined by Cottier et al. 2006), and that can be detected and quantified using data sampled with ADCPs.

Whilst (1) the existence of synchronised DVM in autumn, spring, and early/late winter is well described in the Arctic (Cottier et al. 2006, Benoit et al. 2010, Wallace et al. 2010, Berge et al. 2014), (2) the LVM behaviours of mid-winter have been detected on a pan-Arctic scale (Last et al. 2016), and (3) small-scale vertical migrations have been observed in the mid-winter in the surface layers (Ludvigsen et al. 2018), the factors that determine transition between these differing states are not well understood or quantified. The shift from solar- to lunar-driven responses is only seen during the period of full moon in the darkest part of winter (Last et al. 2016), but the timing of this transition and any dependence on latitude has not been investigated. This paper intends to quantify the cessation of fully synchronised, deep (i.e. >20 m), classic (solar-driven) DVM as the winter progresses, and its re-initiation in spring. Our focus was to quantify how the prevalence of DVM, which has an impact on further predator–prey interactions (Hays 2003) and which plays a part in the flux of carbon to depth (Steinberg et al. 2000, 2002, Takahashi et al. 2009), varies across the Arctic Ocean during the polar night.

MATERIALS AND METHODS

Acoustics

The data set used here (referred to as the panArchive from this point forward) is a collection of data sampled from moored 300 kHz ADCPs (Teledyne RD Instruments) from 58 deployments across the Arctic Ocean (Fig. 1). ADCPs were deployed in an upward-looking configuration. The moored depth of the ADCPs varied from 55 to 311 m, with the ADCPs having a nominal acoustic range of 120 m. Data were averaged into either 4 or 8 m depth bins; the value of bin depth represents the centre of each bin (i.e. the 20 m bin covers the region 18 to 22 m when using 4 m sampling resolution). The time resolution of sampling was between 5 and 60 min. These 300 kHz instruments are most likely to represent mesozooplankton size scatterers (≥5 mm). Large signals might be received from any fish entering the acoustic beam,

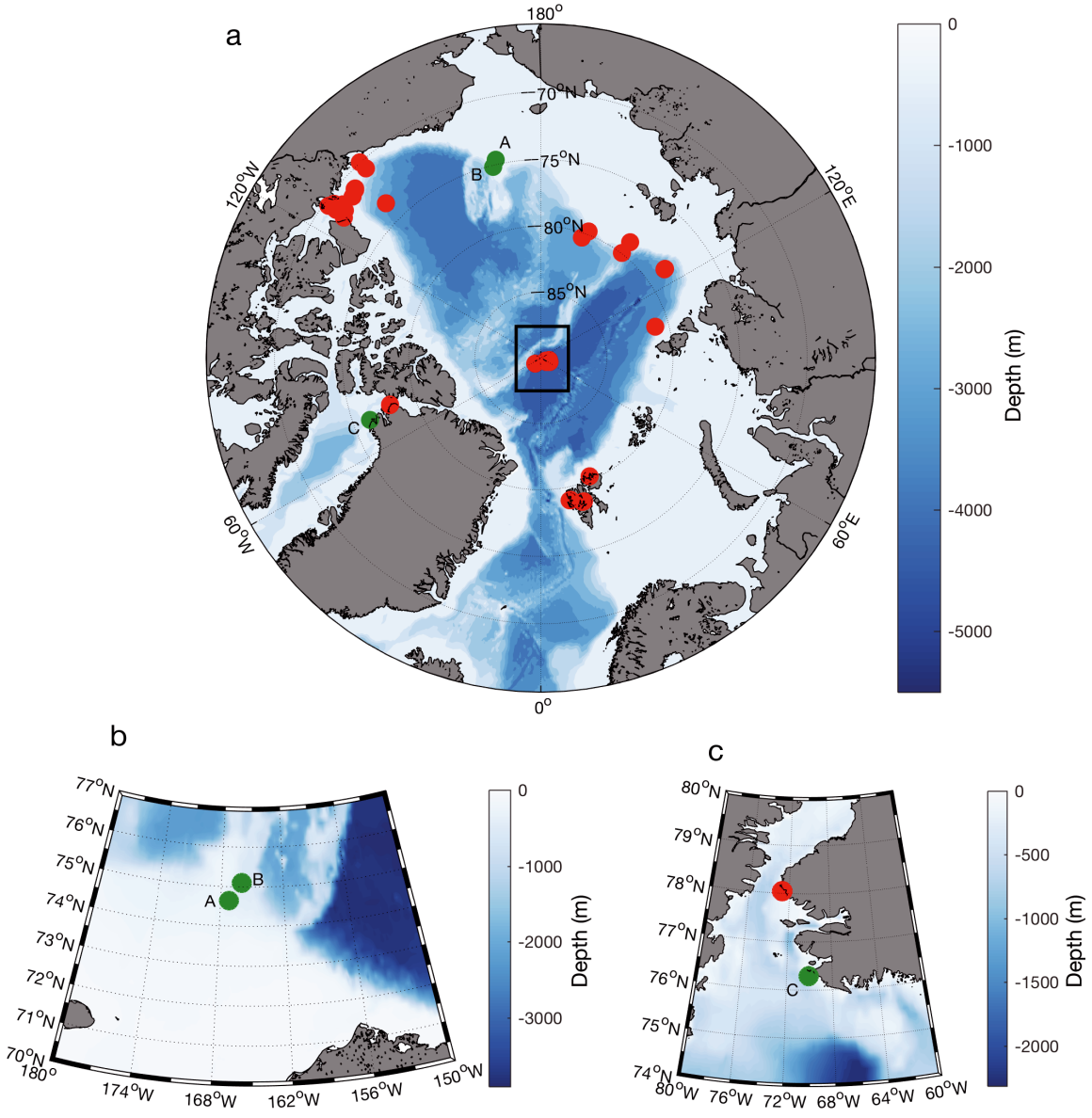

Fig. 1. (a) Acoustic Doppler current profiler (ADCP) mooring locations (n = 58) in the panArchive. Individual moorings are indicated by coloured circles (red and green); green circles (n = 6): moorings used in the sea ice case study; black rectangle: moorings (n = 7) used in the North Pole case study. Full description of the mooring stations and supplementary information can be found in Hobbs (2016). (b,c) Detailed maps of mooring stations used in the sea ice case study (each green circle represents 2 yr of sampling): (b) mooring Stns A and B; (c) mooring Stn C

but these signals are rejected by the ADCPs using an internal data filtering process (RDI 1996). All deployments covered at least one full polar night period (defined as the middle of October to middle of March). The shallowest sections of data (between 6 and 20 m) were discarded due to side-lobe interference of the acoustic beams at the surface boundary. The shallowest depth with available data across all data sets was 20 m. ADCP data were processed to backscatter (S_v; dB re 1 m^{-1}) using methods applied in Hobbs (2016), Last et al. (2016), Geoffroy et al. (2016), and many others, using the sound equation of Deines (1999).

Presentation and analysis of backscatter data

Actograms (Fig. 2) are a means of visualizing daily variations in backscatter at prescribed depths to show the progression of diel behaviours over long periods of time (on the order of months). They were created (process fully described in Last et al. 2016) by stacking 24 h periods of backscatter data from a single depth bin (20 m in these examples) vertically to form a matrix that is 24 h wide on the *x*-axis and 6 mo long on the *y*-axis. The data were then 'double plotted' on the *x*-axis so that 2 sets of the same 24 h of data are shown in horizontal succession. Strong DVM can be seen in the actograms in Fig. 2a,b, particularly in autumn and spring (top and bottom of figures, respectively), characterized by low backscatter in the hours around midday and high backscatter in the hours around midnight. Such a strong acoustic response is caused by vertical migration — populations migrating at the same time and forming a dense sound-scattering layer of high backscatter. The 'V' shapes that are formed in the actograms in Fig. 2a,b are indicative of a response in the DVM behaviour with changing photoperiod, with migrators spending less time each day avoiding the surface as autumn progresses into winter, and more time each day avoiding the surface as winter progresses into spring.

In Fig. 2a, the duration of time spent migrating down each day reduces during late autumn, but the DVM is continuous throughout the year. In Fig. 2b, there is a gap between the apices of the 'V' shapes —

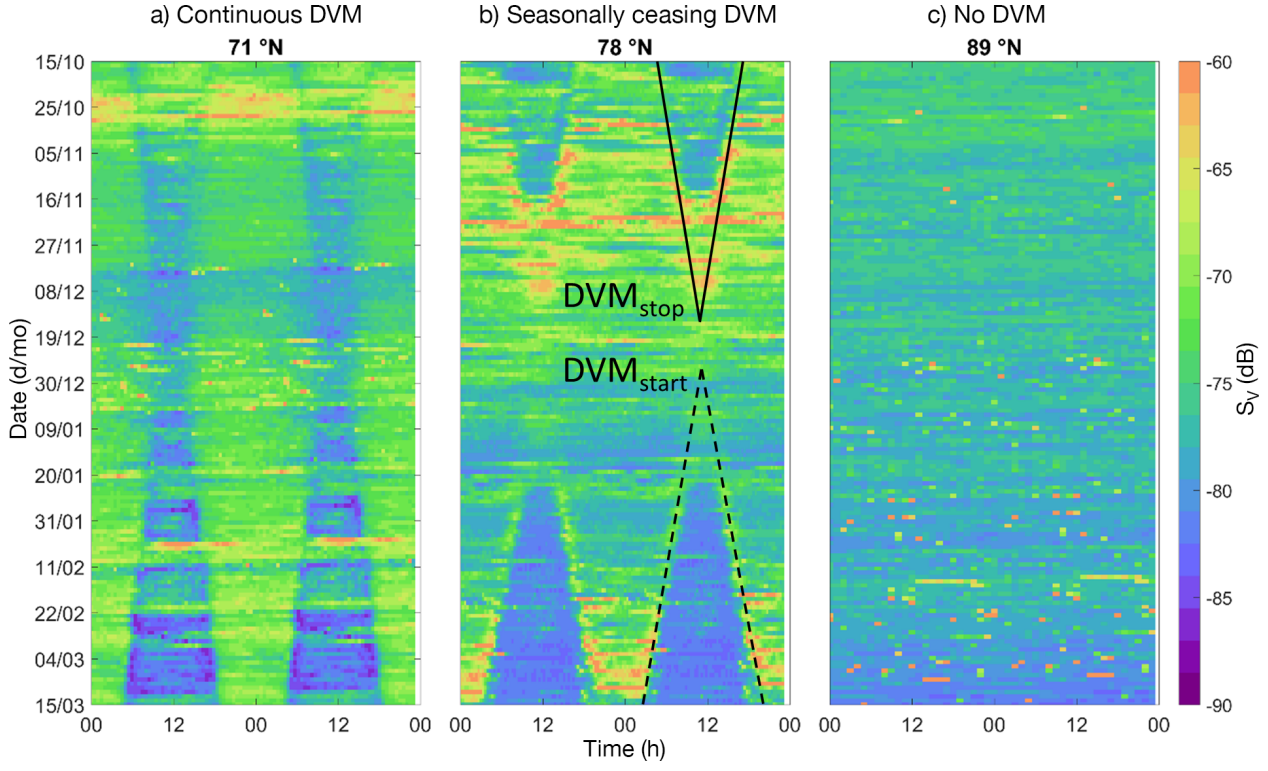

Fig. 2. Actograms at 3 latitudes presenting acoustic backscatter from the 18 to 22 m depth bin, sampled using acoustic Doppler current profilers (ADCPs). Three varying seasonal patterns of diel vertical migration (DVM) are shown: (a) continuous DVM (sampled at 71°N); (b) seasonal cessation of DVM (sampled at 78°N); and (c) no DVM (sampled at 89°N). In (b), lines have been drawn to illustrate the methodology of calculating dates for DVM_{stop} (solid) and DVM_{start} (dashed) using the points at which each pair of lines forms an apex

interpreted as a period of cessation of 'classic' DVM during the polar night at 20 m. Fig. 2c is an example where there is no evidence of DVM at any time of the year. The 3 actograms shown in Fig. 2, using examples from a range of latitudes (71, 78, and 89° N), are illustrative of the 3 types of seasonal DVM behaviour that exist in data from the panArchive: Fig. 2a shows DVM that continues all year round ('continuous DVM'); Fig. 2b shows DVM that ceases for a period during the polar night ('seasonally ceasing DVM'); and Fig. 2c shows no DVM occurring at all ('no DVM'), all plotted using data sampled at 20 m.

Actograms were plotted at the pre-selected depths of 20, 40, and 60 m (not all actograms shown). The data bins closest to these depths were used for plotting 3 actograms for each of the 58 data sets in the panArchive where available. Two factors affected the exact bin depth used: (1) the sampling resolution: each bin depth reflects the centre of a bin either 4 or 8 m in depth, and (2) the installation depth of the ADCP, such that bin depths did not necessarily fall exactly at 20, 40, or 60 m. Only data sets with bin centres at the required depth (±4 m) and which covered the period of the polar night (roughly October to March) were used (n = 50). Each actogram was classified into 1 of the 3 groups described above (continuous DVM, seasonally ceasing DVM or no DVM).

Definition of DVM cessation period

Actograms that were classed as showing seasonally ceasing DVM (exemplified in Fig. 2b) were further analyzed to determine the timing and duration of the gap that appeared between the 'V' apices — i.e. where synchronised, classic DVM ceased at depths greater than 20 m — defined hereafter as the 'DVM cessation period'.

Straight lines were eye-fitted following the method of Tosini (2007) (examples of implementation can be seen in Chabot et al. 2012, Oliver et al. 2012) along the edge of synchronised activity in both autumn and spring, as illustrated in Fig. 2b. The points at which these lines intersect were defined as DVM_{stop} and DVM_{start} in autumn and spring, respectively. Last et al. (2016) found that a monthly lunar migration response can sometimes 'mask' the end of classical DVM. By drawing these lines that define overt DVM activity, the masking of DVM by lunar responses (an example of which can be seen in Fig. 2b close to 24 November) will not affect the date of DVM_{stop}.

Definition of sea ice cover

The presence/absence of sea ice cover (and resulting number of sea ice days) at each ADCP mooring was determined using the ADCP data, following Hyatt et al. (2008), as applied by Wallace et al. (2010). Briefly, the horizontal velocity from 4 ADCP beams was plotted against time, and the region during which the variance in horizontal velocity is minimised was selected as a period of sea ice cover. Whilst this method cannot be used to calculate sea ice thickness, or any other properties of the ice itself (e.g. snow cover), it is appropriate for determining the presence/absence of sea ice cover. The significant advantages of this method are that it provides a reliable measure of sea ice presence at the exact location of each mooring, is exactly comparable between ADCP data sets, and provides information where satellite data is not available (i.e. at the 89° N mooring stations).

In addition to the data on sea ice coverage collected using ADCPs, sea ice concentration data (from Nimbus-7 SMMR and DMSP SSM/I-SSMIS passive microwave data, version 1; Cavalieri et al. 1996) were used for 3 case study mooring locations (highlighted by green circles in Fig. 1), each having been sampled for 2 yr. Sea ice concentration (0 to 100%) data were plotted at 3 d resolution for the period of 1 October to 1 February for each year of ADCP sampling, and the average sea ice concentration at each mooring location (74.64° N, 168.8° W; 75.1° N, 168.0° W; and 76.3° N, 70.1° W) was recorded.

RESULTS

DVM cessation in winter

The cessation of DVM during winter in depths >20 m was seen to be primarily a function of latitude (Fig. 3). South of 77° N, DVM was mostly continuous during the polar night (with 2 exceptions, discussed below). Between 77 and 81° N, DVM ceased for a period during the middle of the polar night. No data are available from the latitude range spanning 81 to 89° N. At stations close to the North Pole (89° N), there was no evidence of DVM at any time of the year. A summary of these latitudinal classifications is shown in Fig. 3a, along with a conceptual summary of the findings (Fig. 3b).

Between latitudes 74 and 77° N, we identified a transition zone in which the cessation in DVM was not defined clearly by latitude alone: the classifica-

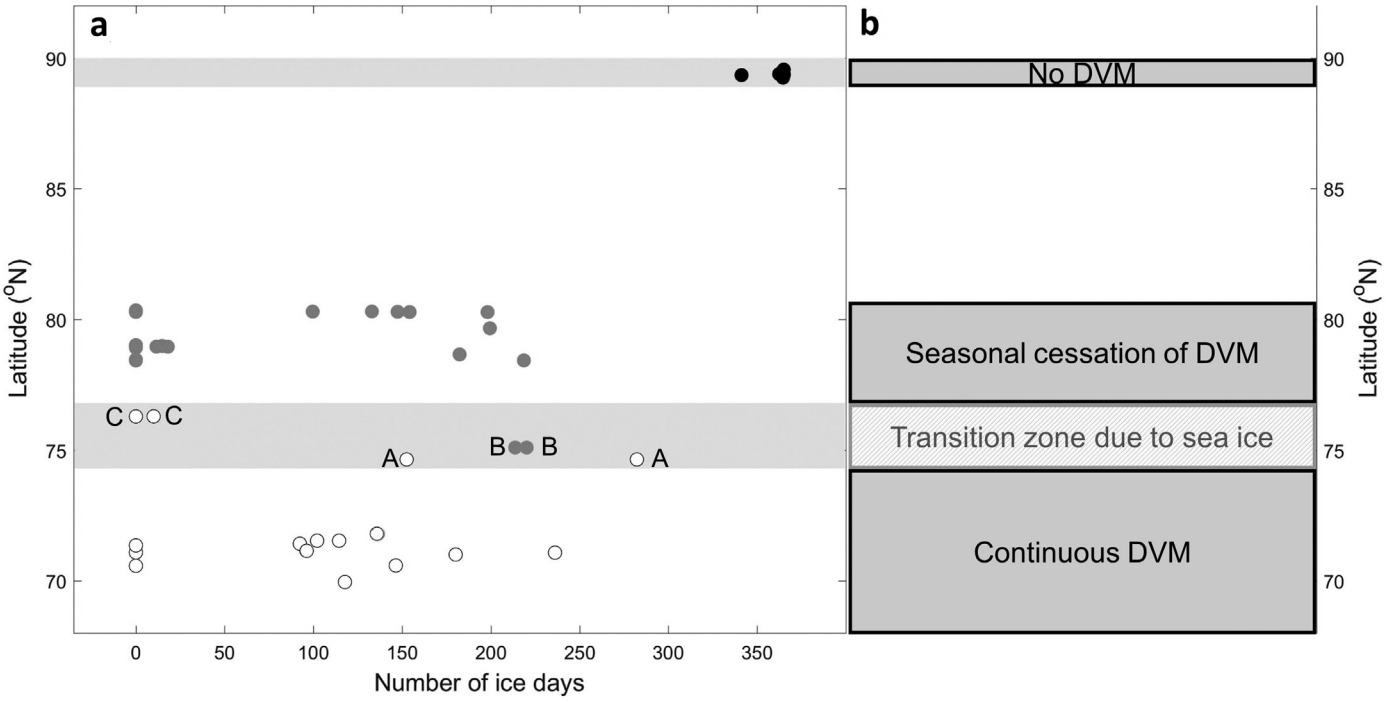

Fig. 3. (a) Classification of panArchive data sets as continuous diel vertical migration (DVM) (white circles), seasonal cessation of DVM (grey circles), and no DVM (black circles) using acoustic Doppler current profiler (ADCP) backscatter data from the closest data bin available to 20 m. Shaded bands show data sets used in 2 case studies: bottom—a sea ice case study in the transition zone (3 case study mooring stations, A, B, and C, are shown); top—an extremely high latitude case study close to the North Pole (~89°N). (b) Conceptual representation of latitudinal variation in seasonal DVM behaviours, summarising the observations in (a)

tion of DVM responses show variation compared to the general latitudinal trend. These 6 data sets (highlighted by the bottom shaded band in Fig. 3a) form a case study into the effect of sea ice on DVM, using the satellite-derived sea ice concentration data.

Sea ice case study

Localized sea ice conditions were seen to affect migrations (Fig. 4). DVM was continuous at 20 m at both mooring Stns A and C in both years. At mooring Stn B, DVM ceased for 17 and 9 d in each year. Sea ice concentration varied between the 6 data sets, with the earliest-forming and highest concentrations of ice at Stn B in 2005–2006 (full-concentration ice formed on 3 November). At Stn B in 2006–2007, full-concentration ice formed more than 1 mo later (9 December), but with some broken ice (>45% concentration) present from the start of October. Mooring Stn A in 2006–2007 had full-concentration ice forming on 31 October, but once formed varied more in its concentration, which did not remain continuously at 100% until 9 December. Mooring Stn A in 2007–2008 had the latest first occurrence of any ice (16 November), and ice remained patchy until reaching 100% concentration on 17 December. At mooring Stn C, relatively few full-concentration ice-covered days were recorded (and satellite-derived data showed that sea ice concentration in the area of the mooring station was generally <100%, with mean concentrations of 65 and 41% in each of the years). In the time leading up to 21 December (the winter solstice, most likely time for any DVM cessation to occur) neither year had experienced a full cover of sea ice (100% concentration).

North Pole case study

At the mooring stations positioned close to the geographic North Pole (89° N), DVM was not observed at any time of the year (Fig. 3). No diel cycle was observed during the autumn equinox (the time of the strongest day/night light cycle), with backscatter variations between midnight and midday being 0.23 dB, in contrast with observations from data sampled at a station at 81° N during the same period

which had backscatter variations of ~10 dB (Fig. 5). Midnight–midday backscatter differences across the whole year were on average 0.0034 (±0.0287, 95% CI) dB when averaged for all 7 yr.

DVM cessation as a function of depth

Data sets in which the backscatter data showed a cessation of DVM in winter (grey circles in Fig. 3) were used to investigate the relationship between depth and the duration of a DVM cessation period (Fig. 6). Grey bars show the mean date of DVM_{stop} and DVM_{start}, with one standard error indicated by black lines. Synchronised DVM ended on 11 December (±3.45 d, 95% CI), 5 December (±2.56 d), and 3 December (±3.08 d) at 20, 40, and 60 m, respectively. At the same depths, DVM started on 6 January (±3.33 d), 10 January (±3.09 d), and 12 January (±3.77 d). Synchronised DVM ended earlier and started later with increasing depth, therefore increasing the duration of the DVM cessation period. DVM ceased for a mean period of 27, 36, and 40 d at 20, 40, and 60 m, respectively. The rate of change in cessation period with depth was 2 d m^{-1} for DVM_{stop} and 1.5 d m^{-1} for DVM_{start}. To investigate the strength of the relationship between DVM cessation and the annual light cycle, the midpoint of these 2 dates was calculated for each depth. The mean dates across all the data sets were 23, 22, and 22 December at 20, 40, and 60 m, respectively.

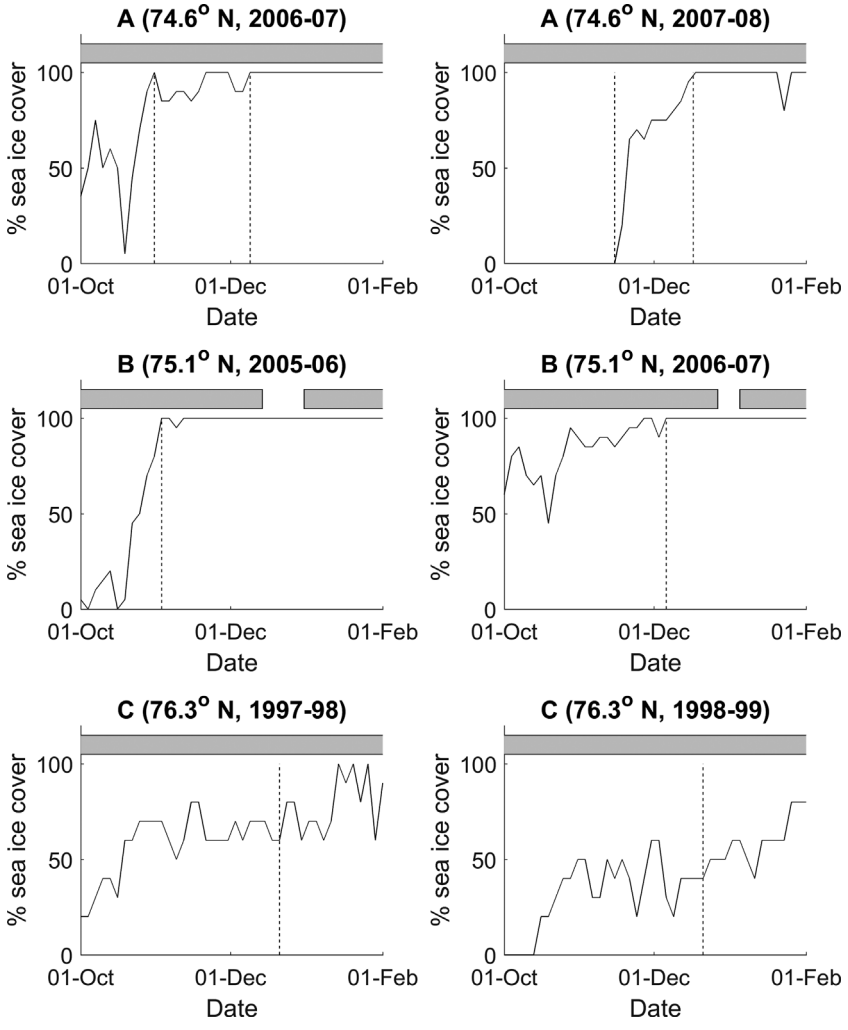

Fig. 4. Effect of localised sea ice on the seasonal cessation of diel vertical migration (DVM) using 3 mooring stations in the 'transition zone' (as per Fig. 3): Stn A: 74.6°N, 167.2°W; Stn B: 75.1°N, 166.0°W; and Stn C: 76.3°N, 70.1°W. Black lines: concentration of sea ice (from Nimbus-7 SMMR and DMSP SSM/I-SSMIS passive microwave data, version 1; Cavalieri et al. 1996) at 3 d resolution from satellite data. Shaded gray bars at the surface indicate the presence of DVM signal at 20 m depth. Continuous bars (such as at mooring Stns A and C) show no cessation of DVM (represented by white dots in Fig. 3); broken bars at Stn B show a cessation of DVM for 17 and 9 d (in 2005–2006 and 2006–2007, respectively). Vertical dashed lines: significant dates in sea ice data, as referred to in the 'Sea ice case study' section

DISCUSSION

We have presented a pan-Arctic assessment of the occurrence and cessation of solar-mediated, synchronised DVM. Fully synchronised DVM in the Arctic ceases for a period in mid-winter at latitudes between 77 and 81° N, or at least becomes shallower than 20 m. South of 77° N, DVM continues throughout the winter due to a continuously perceptible solar irradiance cycle, except during times of high sea ice concentration or early formation of ice, when DVM ceases. At 89° N, no DVM was observed due to a lack of a diel solar cycle at this extremely high latitude. Sea ice concentration is a primary factor limiting DVM throughout the winter and its occurrence results in a DVM 'transition zone' at latitudes between 74 and 77° N. Shading by sea ice presumably reduces DVM in both the depth and duration for which it exists, and this is likely to change in a warming Arctic Ocean via changes in shading and turbidity.

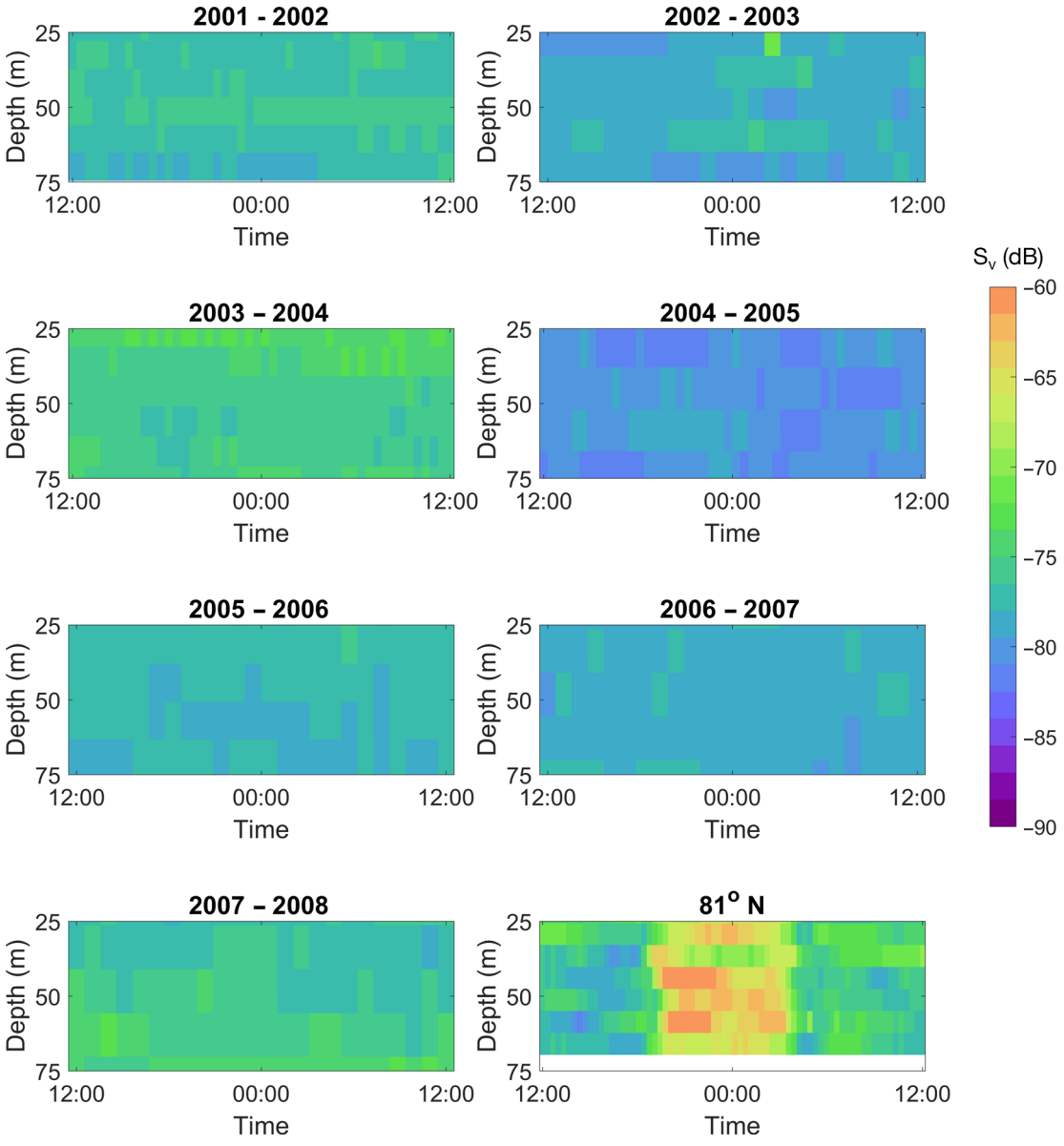

Fig. 5. Echograms of hourly averaged data for the 7 d period (each data point represents the average backscatter at that time across all 7 d) over the autumn equinox (21 September). Plots labelled with years are data sampled at 89°N (North Pole mooring stations, highlighted by the black rectangle in Fig. 1 and top shaded band in Fig. 3a); lower right plot is data sampled at 81°N for comparison. A clear diel vertical migration (DVM) cycle (high backscatter at midnight, low at midday, ~10 dB daily variation) is seen at 81°N compared to 89°N (no observable daily variation, 0.23 dB of maximum variation between midday and midnight)

Overall light availability decreases with water depth due to attenuation by seawater and its particulates. We showed the effect of this attenuation through a variation in the duration of DVM at different depths (Fig. 6), where DVM occurred for longer periods throughout the year at shallower depths. Migrating populations gradually decreased the depth of their migration during late autumn in response to the changing depth of a specific isolume as the sun inclination decreased below the horizon (Bianchi et al. 2013). During this time of no DVM in deeper water, we conclude that migrators spend the hours of daylight migrating to the maximum depth of observed DVM in the actograms, and the hours of darkness in surface waters. During the period of cessation, populations aggregate at the surface where there is no longer a threat of visual predation at any time during a 24 h cycle. This continuous occupation of the surface water during darkness was not possible to observe in the data used in this study (due to

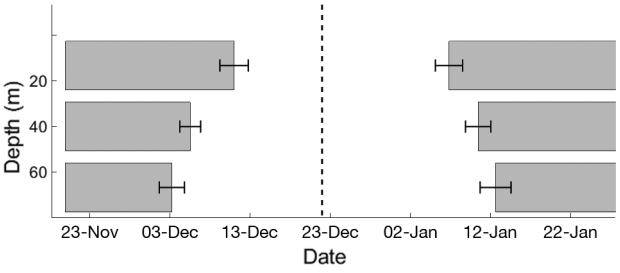

Fig. 6. Mean date of the beginning and end of diel vertical migration behaviour (DVM_{stop} and DVM_{start}) across all data sets that showed seasonal cessation of DVM at all 3 depths (n = 22). Error bars: SE at each depth; vertical dashed line: winter solstice

limitations of ADCP at the air–ocean interface), but we can observe the daytime scattering layer moving from 60, to 40, to 20 m in the actograms as the winter solstice approaches, which logically leads to it becoming shallower than 20 m during the period of DVM cessation. Nevertheless, it is likely that small migrations (with amplitudes <20 m) might still occur in the surface layers shallower than those sampled here (i.e. Ludvigsen et al. 2018).

This depth-related response assumes that the scattering profile does not represent different communities at different depths. In other studies, multiple scattering layers have been observed throughout the water column (Berge et al. 2014, Tarling et al. 2014) which might provide an alternative explanation for the variation in timings of DVM_{stop} and DVM_{start} seen at different depths (i.e. there are different types of scatterers at each depth, and different groups have varying levels of light perceptibility; Cohen et al. 2015). However, the increase in the duration of DVM cessation as a function of depth suggests a depth-varying parameter, such as light, and the consistency in the response within the panArchive data set suggests that the controlling parameter, common across the Arctic, is light rather than community composition which would not necessarily provide such a consistent response. It is worth noting, however, that DVM does not occur in all species that will be observed using the ADCPs, and even within a single species there can be variation in the DVM response between age stages of individuals, and morphological characteristics such as size and colour. Whilst light availability reduces with depth due to attenuation, it also varies spatially due to differences in water quality. Rising temperatures in the Arctic are predicted to increase river run-off (Morison et al. 2012), which will in turn increase turbidity levels. Increased particulate matter in the water will increase light scattering, absorption, and therefore attenuation (Hanelt et al. 2001) and may thereby indirectly reduce the length of the time for which synchronised DVM exists, particularly in areas mostly affected by riverine input (such as the Siberian Shelf).

We have shown that the cessation of DVM in the polar night is controlled by light, with the date of the winter solstice being calculated (within an error range of 2 d) using only observations of migration timings. Whilst prey is also an important driver of DVM (Hays 2003), we found in this analysis that light is the primary controlling parameter, with DVM ceasing during the period of lowest light availability. During this period of cessation, other forms of weaker vertical migrations may still be taking place, e.g. in response to moonlight (Last et al. 2016), unsynchronised migrations where there is no optimal time to feed (Cottier et al. 2006), or migrations that are confined to the upper 20 m (Ludvigsen et al. 2018) that were not detected using this methodology.

The observation of no DVM at 89° N is a novel finding. In agreement with the data presented here, Hobbs (2016) found little periodicity in the data sampled at 89° N compared to other data in the panArchive data set (at least for periodicity in the 19 to 29 h range). Our finding is in agreement with the hypothesis that DVM is principally light controlled (Ringelberg 1999, Ringelberg & van Gool 2003), with the sun not crossing the horizon at all for 6 mo at a time, although LVMs still occur (Last et al. 2016). Whilst we find that DVM is observed up to 81° N, and is not observed at 89° N, we have no understanding of the behaviours that occur between these latitudes due to an absence of data. However, it might be expected that the lack of DVM extends for several degrees south of 89° N since even at 88° N (which includes a total northerly geographical area of 1.57×10^5 km^2), the sun only crosses the horizon for a total of 10 d each year (although it is currently not known how many days per year of a diel solar cycle would be required to initiate DVM).

Sea ice has also been found to modify DVM, principally through the shading effect (though indirect consequences of sea ice such as the effect it has on food, turbidity, and species composition have also been seen to alter the occurrence of DVM; Wallace et al. 2010). Continuous DVM occurred at both the lowest latitude (Stn A) and the highest latitude (Stn C), but not at the mid-latitude (Stn B). Stn C had the lowest sea ice concentration. Patchy, thinner sea ice allows more light to penetrate the water column (Varpe et al. 2015), and this provided enough light to entrain DVM at Stn C. Even when sea ice forms at

the same time of year, the sea ice has a different effect on DVM depending on how concentrated it remains once formed. This was seen in the difference between DVM occurrence at Stn B (2005–2006) and Stn A (2006–2007). At Stn B, sea ice remained at 100% concentration once formed, but fluctuated between 85 and 100% at Stn A. Greater ice concentration at Stn B provided sufficient shading to for DVM to cease during the winter, whereas DVM continued at Stn A. We also found that sea ice does not have to be at 100% concentration to contribute to DVM cessation, providing it forms early enough. At Stn B (2006–2007), DVM ceased for a period of 9 d despite a late formation of full-concentration sea ice. However, for 2 mo prior to this time, sea ice cover was consistently above 45%. The extensive period of shading caused by this cover resulted in DVM cessation. Sea ice that never reaches 100% cover is unlikely to cause a cessation in DVM. We saw evidence of this at Stn C, where, despite being sampled at the highest latitude of all 3 sea ice case study stations, DVM continued throughout winter. At locations within the 'transition zone' latitudes, early ice formation or sea ice cover of high, continuous concentrations throughout the late autumn shades the incoming sunlight, which presumably does not provide a strong enough photoperiodic cycle to maintain overt DVM. Conversely, in years where sea ice forms later, is at lower concentrations, or does not form a continuous/consolidated ice pack for some time, DVM was continuous throughout the winter.

Sea ice in the Arctic is currently experiencing a decline in extent, concentration, and thickness (Serreze & Stroeve 2015). If the results presented here are representative of the Arctic Ocean as a whole, we predict that decreasing sea ice cover will lead to increased DVM (in terms of duration and depth extent) throughout the polar night. Consequently, this might lead to greater flux of carbon to depth (Darnis et al. 2017). Although this increase might be viewed as a positive mitigation against the mostly negative ecological consequences of climate change and sea ice reduction (for example: habitat loss, Laidre et al. 2015; ocean acidification, Bates & Mathis 2009; changes in phenology, Ji et al. 2013, Ramírez et al. 2017), it should be noted that increases in light availability might also increase the success of visual predation (Varpe et al. 2015) or alter other ecosystem interactions, meaning that direct predictions about the effects of increasing DVM are hard to quantify. The continuation or cessation of full-depth, synchronous DVM has implications for the wider ecosystem through carbon flux (Darnis et al. 2017) and predator–prey interactions (Brierley 2014), and its prevalence and likelihood of change in the future is important to understand within the context of the Arctic Ocean ecosystem.

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